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TAXONOMIC OVERVIEW OF *DIPLACUS* SECT. *DIPLACUS* (PHRYMACEAE)

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ABSTRACT

A study of *Diplacus* sect. *Diplacus* recognizes twelve taxa of the USA at specific rank: D. *aridus*, *D. aurantiacus*, **Diplacus x australis** (McMinn ex Munz) Tulig, **comb. nov.**, *D. calycinus*, *D. clevelandii*, *D. grandiflorus*, *D.* x *linearis* (Benth.) Greene, *D.* x *lompocensis* McMinn *D. longiflorus*, *D. parviflorus*, *D. puniceus*, and *D. rutilus*. A thirteenth species, *D. stellatus*, is an endemic of Cedros Island, Baja California. The hypothesized hybrid taxa appear to function in the same way as others recognized at specific rank. A key to the taxa, distribution maps, and formal nomenclatural summaries are included.

KEY WORDS: *Diplacus, Mimulus* sect. *Diplacus*, *Diplacus aurantiacus*, Phrymaceae

Various botanists have studied the primarily Californian group of *Mimulus* species characterized by sessile to subsessile flowers, parietal placentation, a mostly shrubby or subshrubby habit and perennial duration, and distribution from northern Baja California to southern Oregon. All are at diploid level, $n = 10$. This group has sometimes been treated at generic rank (as *Diplacus* Nutt.) but recent molecular-phylogenetic studies (Beardsley et al. 2004) indicate that they are derived from species of annual duration and nested within the cladistic topology of a more broadly conceived *Diplacus* — they are appropriately regarded as sect. *Diplacus*. Formal nomenclature for the whole genus and rationale for its separation from *Mimulus* L. sensu stricto are presented by Barker et al. (2012). Thompson (2005) treated the whole group (*Diplacus*, including sect. *Diplacus*) as *Mimulus* subg. *Schizoplacus* A.L. Grant.

The taxonomy of sect. *Diplacus* at species and infraspecific rank has been controversial. McMinn (1951a) retained the group at generic rank and recognized fourteen species. Beeks (1962) had similar concepts of species, noting that they were distinct morphologically and ecologically. At another extreme, Thompson (1993, 2005, 2012) has recognized only two species (as *Mimulus clevelandii* and *M. aurantiacus*, monotypic and with 6 infraspecific taxa, respectively), emphasizing high crossability of all taxa and perceived hybridization and intergradation. The present account, which recognizes thirteen species or species-like entities (three of them may be hybrid in origin), is closer in concept to those of McMinn and Beeks, as well as to those of Grant (1924), Pennell (1951), and Munz (1973, 1974), who treated the species within *Mimulus*.

The first author of the present account studied sect. *Diplacus* (Tulig 2000; Tulig & Clark 2000; using nomenclature within *Mimulus*, modified here to *Diplacus*), using 953 plants sampled from 155 locations in California (Fig. 1; see Tulig 2000 for precise localities) chosen to represent the essential geographic range of all named taxa (except for *D. stellatus* from Baja California). A fuller extent of populations representing sect. *Diplacus* is shown by Thompson (2005), although some taxa recognized here are not shown by him as separate entities, and by McMinn (1951a). Plant

identification was based primarily on the keys of Munz (1973), with additional reference to McMinn (1951a) and specimens at RSA. Measurements of floral and foliar characters using digital calipers were made on the uppermost mature flower and subtending leaf of a randomly chosen branch. Three flowers per plant were measured during the 1999 season to address within-plant variation, and one flower per plant was measured during the 2000 season. Vouchers of populations are deposited at RSA and pressed specimens of each plant sampled are at CSPU.

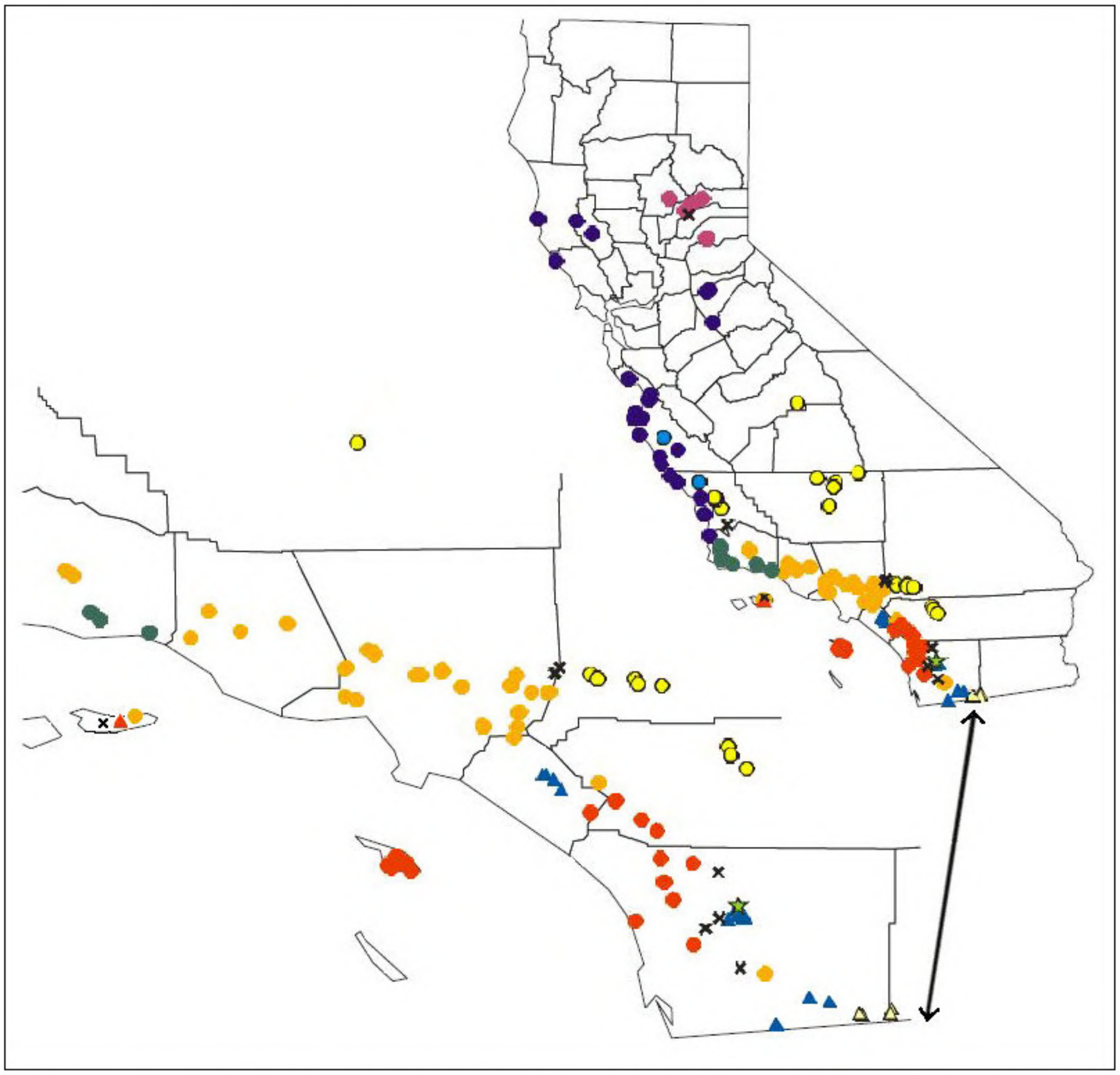

Figure 1. Location of collection sites for the 1999 and 2000 field seasons (Tulig 2000). Dark purple circles–*D. aurantiacus*; light blue circles–D. x *linearis*; purple circles–D. *grandiflorus*; green circles–*D.* x *lompocensis*; orange circles–*D. longiflorus*; red circles–*D. puniceus*; red triangles–D.*parviflorus*; yellow circles–*D. calycinus*; blue triangles–*D.* x *australis*; yellow triangles–*D. aridus*; green star–*D. clevelandii*; black x–hybrid or undetermined population. Also see Figs. 4 and 5.

Data were analyzed by principal components analysis (Fig. 2) and discriminant function analysis (Fig 3). Both analyses distinguished four major groups: (1) *Diplacus clevelandii*, (2) *D. aridus*, (3) taxa with large corollas — *D. grandiflorus*, D. *longiflorus*, and *D. calycinus*, and (4) taxa

with relatively small corollas — *D. puniceus*, *D. parviflorus*, and *D. aurantiacus*. Within each group, geographic ranges further distinguish the taxa and clear separations can be made between most taxa based on quantitative and qualitative morphological characters. *Diplacus stellatus* is an endemic of Cedros Island in Baja California, Mexico, and was not included in the Tulig studies but is included here in the fourth group on the basis of morphology — Thompson (2005) treated *D. stellatus* as a synonym of *Mimulus aurantiacus* var. *auranticus*.

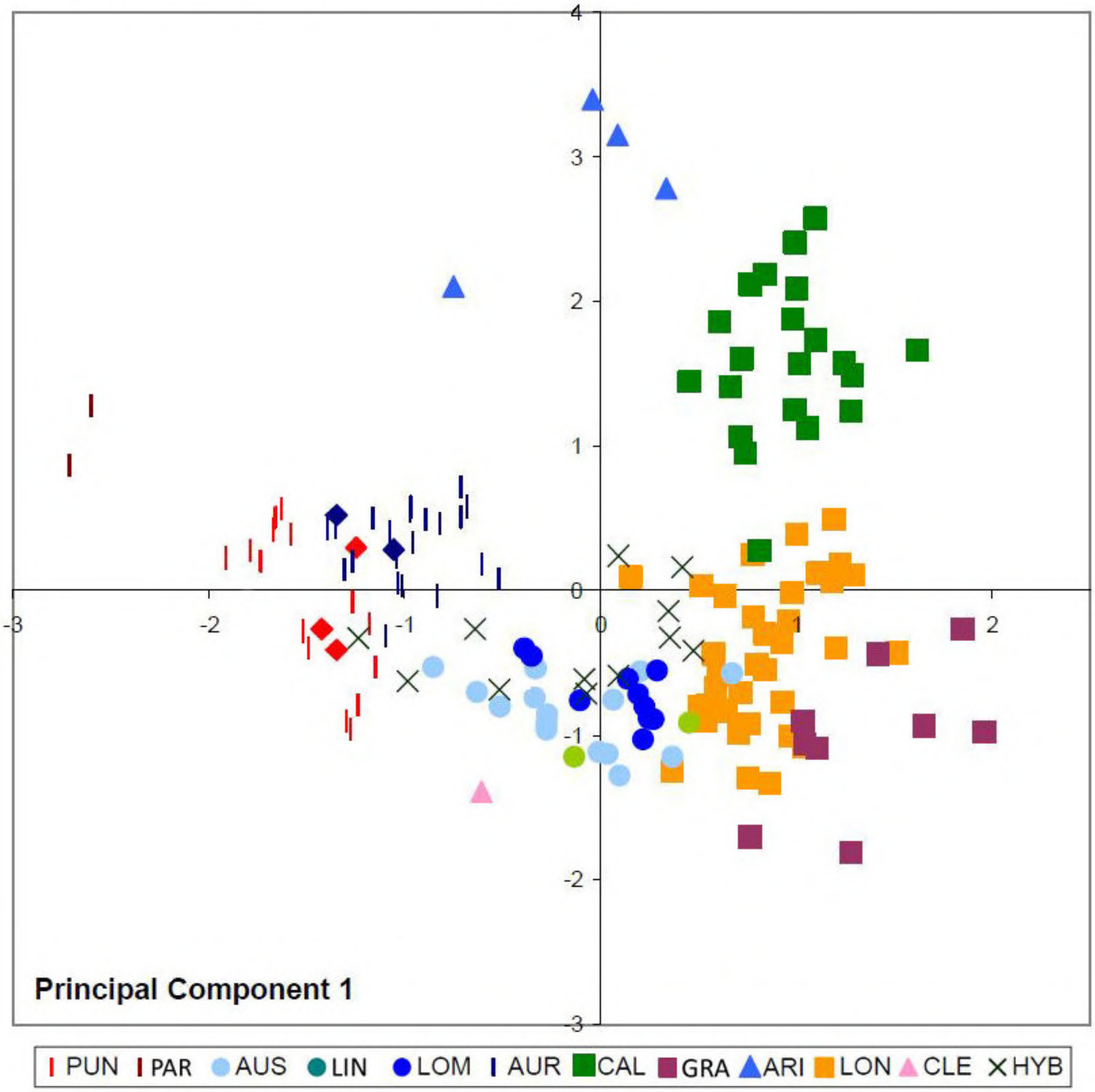

Figure 2. Plot of first two principal components of population means, representing 75.8% of the variation. HYB refers to populations that could not be assigned to a single taxon.

The first three principal components (PCs) account for 85.8% of the total variance of the data (59.6, 16.2, and 9.7% respectively for PC1, PC2, and PC3). PC1 has the highest loadings for all of the corolla features, especially "length across bottom lobes," "apex of upper corolla lobe to outer sinus," and "opening of throat," and high negative loadings for filament lengths. PC2 has the highest loadings for corolla tube length, calyx measurements, and style length and high negative loadings for numerous corolla features. PC3 has the highest loadings for filament lengths and style length.

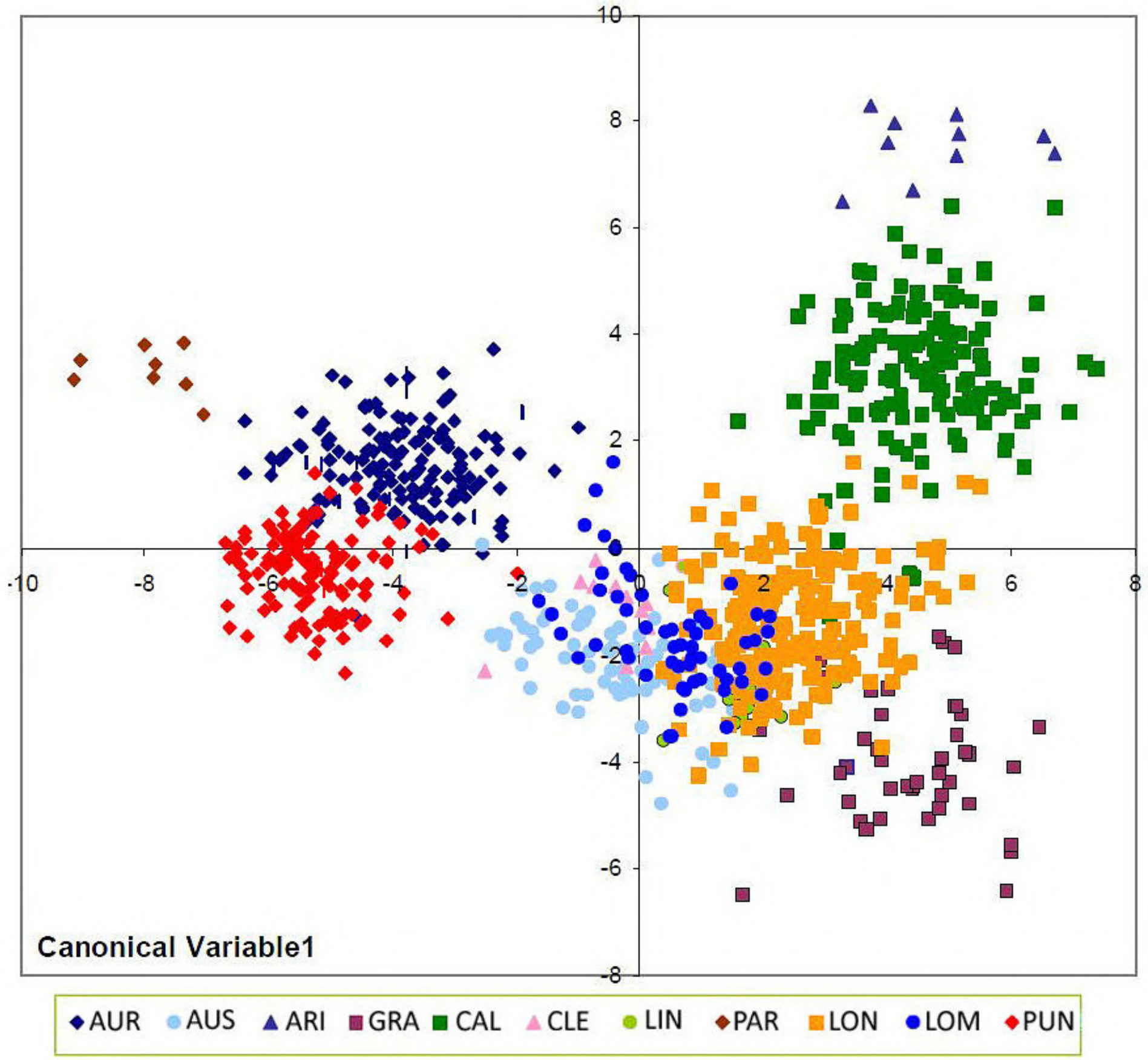

Figure 3. Plot of first two canonical variables of individual plants from the discriminant function analysis.

The first three canonical variables (CVs) account for 90.9% of the variance of the data (64.1, 22.6, and 6.9% respectively). Corolla tube length accounts for most of the variation in CV1 separating the same small and large flowered groups as in the PCA. Corolla tube length was also high on CV2, as well as the corolla features "width of lower center lobe" and "opening of throat," and calyx height. Characters loading highest on CV3 were both calyx features and style length. The scatter plot of the first two canonical variables is similar to that of the PCA except for the position of *M. aridus* which is placed high on both CV1 and CV2 because of its long corolla tube length.

Species concepts and hybridization in sect. Diplacus

In discussing the rationale for his taxonomic concepts regarding sect. *Diplacus*, Thompson (2005, p. 150), noted this: "*Mimulus aurantiacus* shows the most complex variation patterns found in subg. *Schizoplacus*; hybridization occurs wherever any two varieties come together. I have attempted to summarize some of these patterns with as much detail as possible on the distribution maps (Figs. 63-65). A large proportion of specimens are intermediate to some degree and some of these may not

easily key to a recognized variety. Hybrids seem to be sufficiently fertile to allow considerable backcrossing to occur within each hybrid zone, commonly resulting in a complete range of intermediates. The hybrid intermediates have no distinguishing features of their own and very few characters separate the varieties. None of the varieties are geographically isolated from the others, and all have produced naturally occurring intermediates with at least one other variety. I have therefore chosen to accommodate the minimal diversity of this complex among varieties, rather than among species."

In addition to Thompson's view of the variation patterns, he emphasized practical aspects of producing a classification (p. 25). "The intermediates recognized in this work (which often show highly variable or clinal morphological variation between the putative parents) are geographically where we would expect them to be; recognizing them as intermediates or hybrids, rather than as new taxa, increases our understanding of this group and strengthens the classification by making the keys and descriptions work easily for the vast majority of material. The intermediates have very few, if any, unique characteristics, a situation that would cause serious difficulties in writing keys and descriptions, if they were to be recognized as distinct taxa. I must embrace a practical morphological species concept, if this monograph is to be favorably received."

In accounting for his divergence earlier taxonomic concepts (presumably alluding to Munz and others), Thompson observed that earlier studies were "based on little or no original work beyond that provided by Grant (1925)." He did credit McMinn, however, with original work but noted (p. 3) that "unfortunately, the distribution maps provided in McMinn's paper did not show adequately the intricate patterns of hybridization and introgression linking most of the taxa; the same is true of the maps in later work by Beeks (1962)." Thompson also pointed out an ambiguity in McMinn's application of species concept that appears to have linked their two treatments.

McMinn (1951a, p. 34) observed the following: "I have chosen to treat all these field entities (taxa) simply as binomials. Inasmuch as binomials to most botanists indicate species, I have endeavored not to use the word species when writing of these various entities. I must point out, however, that if sterility and geographical distribution tests were the main criteria applied in delimiting species and subspecies, then the field entities of the genus *Diplacus* probably would be classified as two taxonomic species [*D. aurantiacus* and *D. clevelandii*], eleven subspecies, and numerous hybrids." Except for this caveat, however, he treated 14 taxa exactly in the format of species, even describing "4. *Diplacus lompocensis* sp. nov." — thus it appears that McMinn (1951a and also in 1951b) was not satisfied with simply "sterility and geographical distribution tests" in his working and practical concept of *Diplacus* species.

The studies of Tulig, which were not cited or alluded to by Thompson, conclude with a different perspective, more similar (in recognizing more than two species) to those of previous students of the group. Each of the taxa of sect. *Diplacus* has a distinct geographic range and for the most part is clearly defined (Fig. 4), and throughout most of the range of sect. *Diplacus*, hybridization appears to be limited. Much of the taxonomic confusion in the group can be attributed to introgression and hybridization in southern California, occurring mostly at the overlap in distribution of *D. aurantiacus*, *D. puniceus*, *D. australis*, *D. longiflorus*, and *D. calycinus* (Fig. 5). These hybrid/introgressive populations are often characterized by a wide range of corolla colors within and between plants and floral features intermediate to their putative parents.

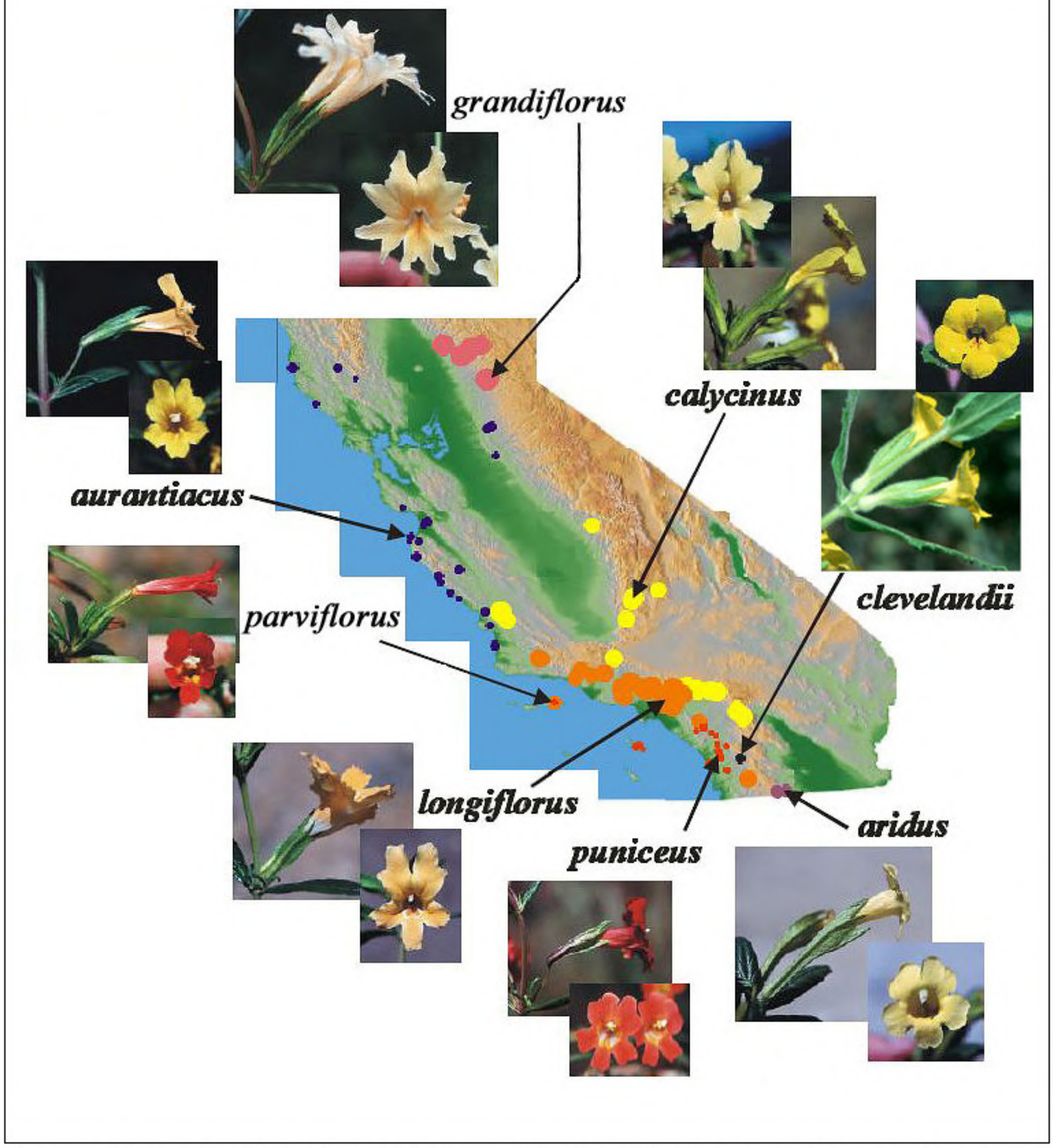

Figure 4. Geographic distribution of *Diplacus* species in California (representing populations studied by Tulig, see Fig. 1). *Diplacus rutilus* is not included in Figure 4 but is treated here as distinct.

Sect. Diplacus is well adapted to dry environments and rock crevices, and the expansion of roads into inner mountain regions has increased the frequency of hybridization. Hybrid populations are repeatedly found along road cuts, as noted here and by others (McMinn 1951a; Beeks 1963; Waayers 1996) and in some areas, hybrids seem to be restricted to road cuts, where they frequently have been collected. The view here emphasizes that blurred boundaries between species have arisen in large part because of zones of sympatry created by human disturbance. The entities are recognized as morphologically distinct and with distinct geographic ranges and as producing intermediates through hybridization only in relatively narrow boundary regions.

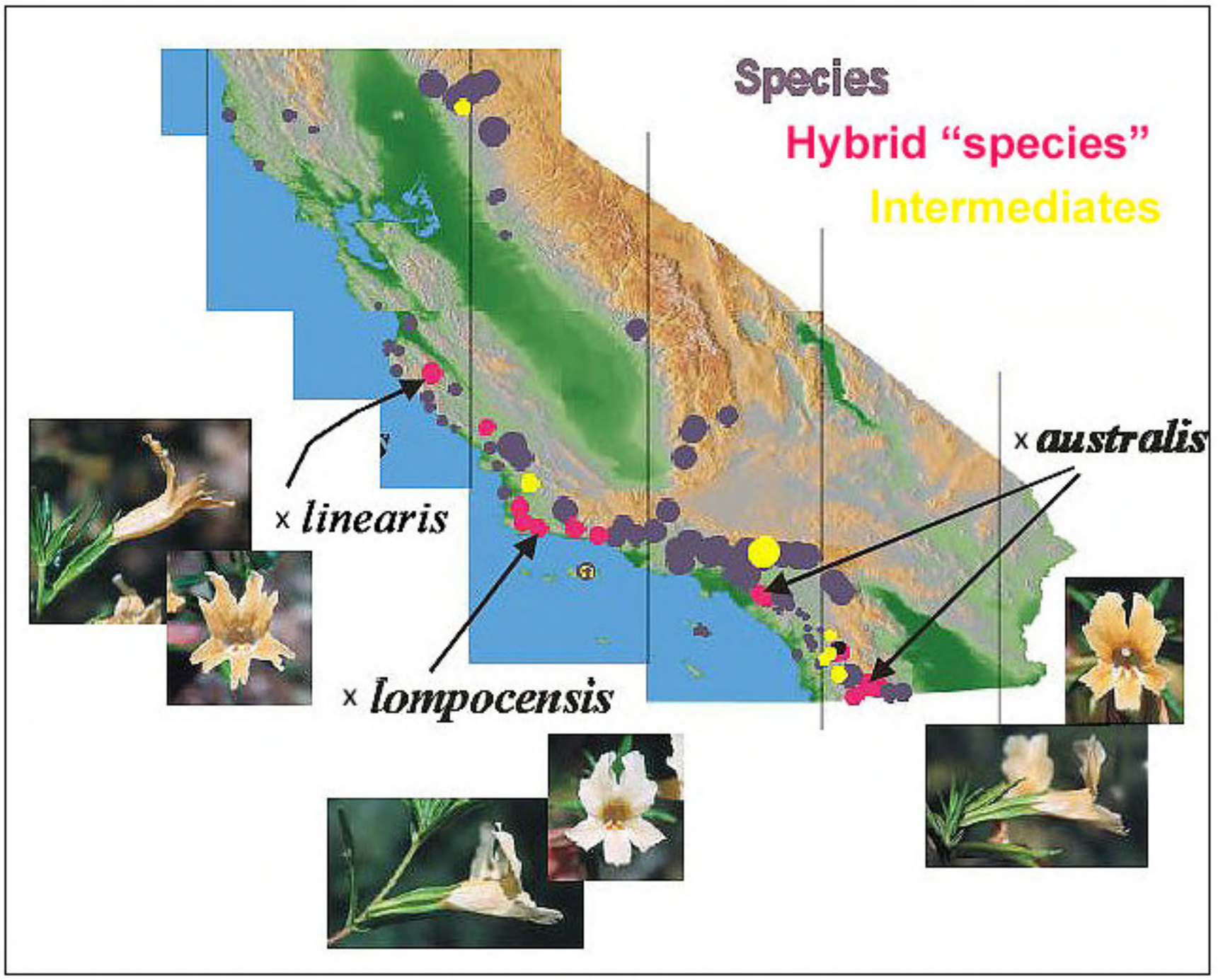

Figure 5. Geographic distribution of *Diplacus* hybrids in California (representing populations studied by Tulig, see Fig. 1).

In the analyses of Tulig (2000), in addition to the entities interpreted as species, three others were consistently distinguished: *Diplacus lompocensis* (*Mimulus aurantiacus* var. *lompocensis*), *Diplacus australis* (*Mimulus aurantiacus* var. *australis*), and *D. linearis* (*Mimulus bifidus* subsp. *fasciculatus*). Each of these appears to be of hybrid origin and is formally treated below. *Diplacus* × *lompocensis* and *D.* × *australis* are intermediate between the large-flowered taxa and small-flowered taxa; *D. linearis* is more similar to the large-flowered taxa.

McMinn recognized essentially the same species as here but included as species those treated here as hybrids — *D. lompocensis*, *D. australis*, and *D. linearis* (as well as *D. fasciculatus* as a distinct entity). He also recognized *D. rutilis* as distinct — it is tentatively placed here within *D. longiflorus* (see comments below). His study included intensive field, and herbarium, and garden study as well as a broad range of artificial crosses.

Beeks (1962) studied only mainland species of southern California, recognizing *Diplacus aridus*, *D. clevelandii*, *D. calycinus*, *D. longiflorus*, and *D. puniceus*. Judging from his species concept, he probably also would have recognized species generally consistent with the taxonomy of McMinn and Tulig. He noted (p. 120) that "When compared regionally, populations of uniform *Diplacus* exhibit conspicuous discontinuities that justifiably allow their recognition as taxonomic units. ... The breakdown of ecological isolation and the occurrence of introgressive hybridization are

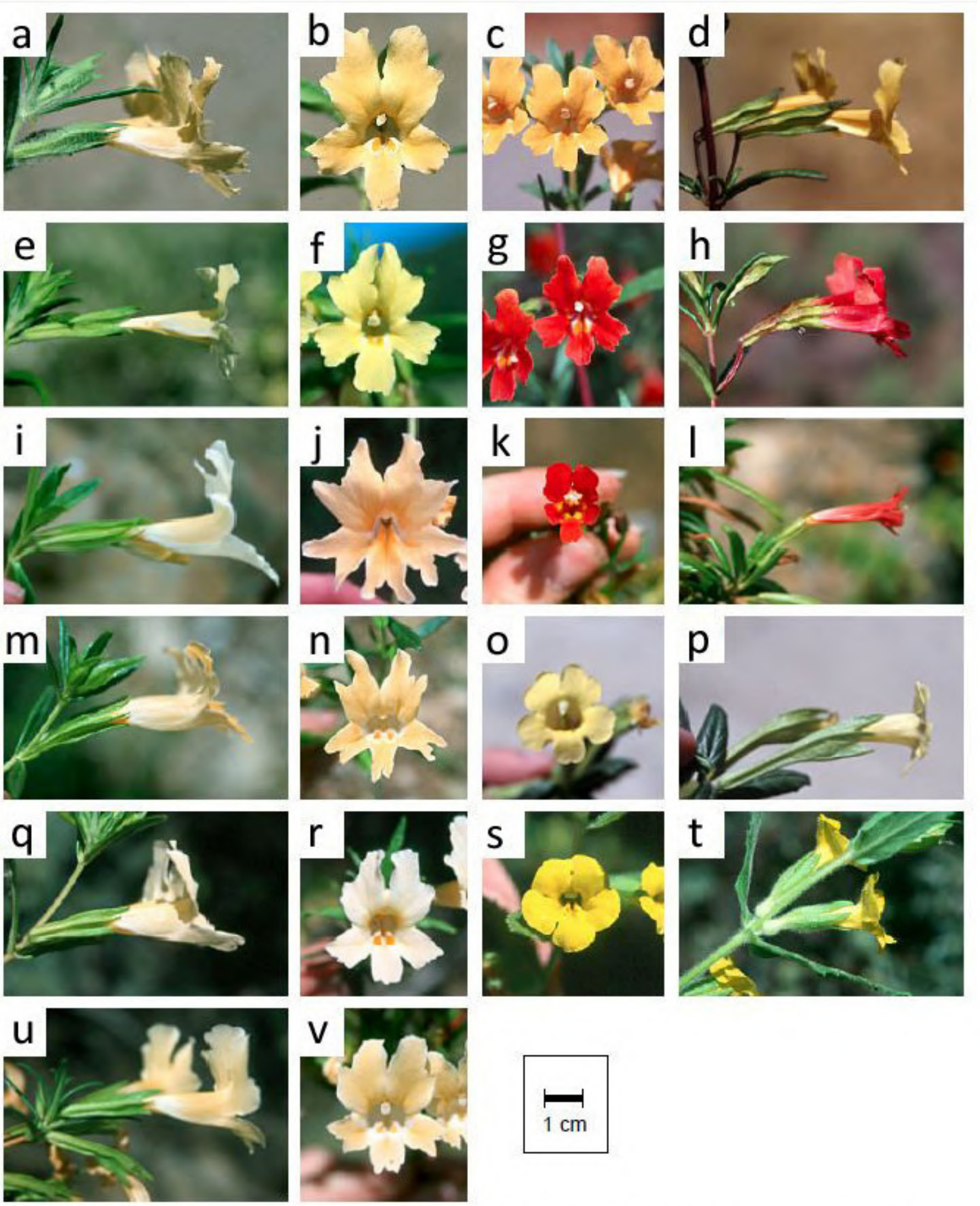

Figure 6. *Diplacus* flowers in face and side view. **a_b** *D. longiflorus*; **c_d** *D. aurantiacus*; **e_f** *D. calycinus*; **g_h** *D. puniceus*; **i_j** *D. grandiflorus*; **k_l** *D. parviflorus*; **m_n** *D.* × *linearis*; **o_p** *D. aridus*; **q_r** *D.* × *lompocensis*; **s_t** *D. clevelandii*; **u_v** *D.* × *australis*. *Diplacus rutilus* is not included.

important causes of populational variability. Interspecific hybridization along the zone of species contact is followed by introgression into the populations. Ecologically open habitats allow extreme recombinants to succeed."

Differences in coadapted pollination systems

In a study of floral isolation between ornithophilous and sphingophilous species, Verne Grant (1993) recognized eight species of *Diplacus* — *D. parviflorus*, *D. puniceus*, *D. longiflorus*, and *D. aurantiacus* are hummingbird-pollinated, while *D. calycinus* and *D. aridus* and hawkmoth-pollinated. *Diplacus clevelandii*, which he interpreted as the most primitive member of the group, is bee-pollinated. He did not have information about *D. stellatus* or *D. grandiflorus*, but the latter appears to be hawkmoth-pollinated, based on its morphology (many good photos available on the internet). *Diplacus stellatus* is closely similar to *D. aurantiacus* and perhaps also is hummingbird -pollinated.

The ornithophilous flowers have red to orangish corollas, daytime nectar production, and relatively shorter and broader corolla tubes (corresponding to hummingbird mouthparts). The sphingophilous flowers have pale-colored corollas, vespertine and nocturnal nectar production, and long and narrow floral tubes (suitable for a long slender proboscis) (Fig. 6). The flowers are structurally adapted for one or the other pollinator type, and foraging behavior of the pollinators is correspondingly adjusted to recognize the interspecific floral differences.

Hummingbirds, however, sometimes visit sphingophilous flowers, hawkmoths sometimes visit ornithophilous flowers, and bees often visit both types of flowers. Thus, secondary pollinators may cross-pollinate the contrasting species, and hybrids and hybrid populations have flowers of intermediate structure that can be visited and pollinated successfully by both hummingbirds and hawkmoths.

The ornithophilous taxa of *Diplacus* are, among themselves, mostly allopatric, as also are the sphingophilous taxa, and Grant surmised that the species of each group arose through allopatric speciation that includes a stage of geographical isolation. "It seems likely that the ancestral species in each plant group developed an ornithophilous pollination race in one geographical area that was favorable for hummingbird pollination and a sphingophilous pollination race in another geographically isolated area that was favorable for sphingophily. Continued divergence with respect to pollination and secular ecological conditions led the divergent branches to the level of externally isolated species, and range expansions brought about sympatric overlap" (Grant 1993, p. 7732).

Streisfeld and Kohn (2005, 2006) studied pollination of *Diplacus* in San Diego County and concluded, in contrast to Grant, at least in this instance, that selection may have caused divergence in flower color in the absence of geographic barriers to gene flow. They found a sharp geographic transition between the coastal red-flowered plants (*D. puniceus*) and the inland yellow-orange-flowered plants (identified here as *D. longiflorus*, see detailed comments below, but by Streisfeld and Kohn as *D.* x *australis*), with a narrow zone of transition (ca. 20 kilometers wide) at their parapatric boundary. The inland and coastal plants also are distinct in corolla tube length and width and volume of nectar production, but corolla color is the most highly divergent feature. Yellow-flowered plants are absent from the western (coastal) region and red-flowered plants are absent from the eastern side of the cline. Pure phenotypes occur in the transition area but intermediate flower colors through hybridization occur there and not elsewhere.

In contrast, however, to the sharp differentiation in corolla color between *Diplacus puniceus* and *D.* x *longiflorus*, genetic differentiation between the two entities at neutral marker loci is far less pronounced — consistent with the hypothesis that current or recent natural selection maintains the steep cline in flower color despite gene flow (Streisfeld & Kohn 2005). The apparent weak neutral

divergence argues against recent secondary contact after a long period of allopatry. Still, in a significant caveat, (p. 2558), they allowed that "Grant's (1993b) contention that red and yellow floral races of *M. aurantiacus* diverged in allopatry may still be accurate, but either the time in allopatry was too short for much neutral divergence to arise, or secondary contact is old, and the cline in flower color has been maintained after secondary contact by selection."

Conservation implications

Recognition of the morphological geographical boundaries of evolutionary entities and the rank at which the taxa are treated are significant in conservation of this group. The only species currently listed as rare by the California Native Plant Society (2012) are *Diplacus aridus* and *D. parviflorus* (and at species rank, in contrast to Thompson's taxonomy) and *D. clevelandii*. *Diplacus aridus* is ecologically distinct and has a limited distribution in San Diego county and northern Baja California. *Diplacus parviflorus* is restricted to the Channel Islands, where ecosystems have been heavily damaged by feral animals.

Plants of sect. *Diplacus* are widely and relatively easily cultivated. Accurate identifications plants already in cultivation will be significant and also may better inform appropriate plantings for species needing attention for conservation.

DIPLACUS sect. **DIPLACUS**

Diplacus Nutt., Ann. Nat. Hist. 1: 137. Apr 1838. *Mimulus* sect. *Diplacus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. **LECTOTYPE SPECIES** (Thompson 2005, p. 25): *Diplacus glutinosus* (Wendland) Nutt. = *Diplacus aurantiacus* (Curtis) Jeps.

In the nomenclatural citations below, distribution of types is mostly according to McMinn (1951a) and Thompson (2005). A few types (depositions) have been added and all confirmations of observation (e.g., "digital image!") are from the present study.

KEY TO THE SPECIES

1. Rhizomatous subshrubs, stems basally woody, distally herbaceous; plants villous-glandular; leaf blades irregularly dentate, finely pubescent-glandular on both surfaces; corollas deep yellow, lobes all about equally joined; capsules 9–12 mm ..... 1. **Diplacus clevelandii**

1. Taprooted shrubs, stems extensively woody; plants glutinous, often with evident stipitate-glandular hairs; leaf blades dentate to entire, not glandular-pubescent on upper surface; corollas red to pale yellow or orange, upper lobes united 1/3–1/2 their length; capsules 12–25 mm.

2. Corollas red to scarlet, throats nearly cylindric and decurved; stigmas and anthers of the longer filaments exserted.

3. Calyces villous to hirsute-villous ..... 11. **Diplacus rutilus**

3. Calyces glabrous.

4. Leaf blades ovate-oblong, apically rounded; corollas strongly decurved, lobes subequal, only slightly if at all notched; Channel Islands ..... 8. **Diplacus parviflorus**

4. Leaf blades linear-lanceolate, apically acute; corollas slightly decurved, lobes unequal and notched; mainland ..... 9. **Diplacus puniceus**

2. Corollas yellow to salmon-colored or orange, throats campanulate, straight to slightly curved; anthers and usually the stigmas included.

5. Calyces 35–40 mm at maturity, tubes distinctly broadened-inflated distally; corolla throats broadly campanulate, ca. half as long as the narrow tube; plants mostly 2–4 dm ..... 2. **Diplacus aridus**

5. Calyces 20–30 mm at maturity, tubes only slightly broadened distally; corolla throats narrowly campanulate, ca. as long as the narrow tube; plants mostly 4–30 dm.

6. Upper corolla lobes deeply notched and appearing bilobed.

7. Leaf blades elliptic-oblong, 8–15 mm wide, apically obtuse to rounded, glabrous abaxially; corolla tube-throat 50–65 mm, lobes notched 1/4–1/2 their depth; central Sierra Nevada ..... 5. **Diplacus grandiflorus**

7. Leaf blades linear-lanceolate, 3–5 mm wide, apically acute, stellate-pubescent to glabrous abaxially; corolla tube-throat mostly 45–55 mm, lobes notched less than 1/4 their depth; coastal ranges ..... 6. **Diplacus x linearis**

6. Upper corolla lobes retuse or shallowly notched to entire or nearly so.

8. Calyces villous to hirsute-villous; leaf blades abaxially villous with a mix of stellate hairs and relatively longer unbranched hairs.

9. Corollas cream to light yellow, tube-throat 48–55 mm; styles 38–46 mm 7. **Diplacus calycinus**

9. Corollas salmon, tube-throat 40–48 mm; styles 28–37 mm ..... 10. **Diplacus longiflorus**

8. Calyces glandular-puberulent to glabrate or glabrous; leaf blades abaxially glabrous or stellate-pubescent, mostly without unbranched hairs.

10. Corollas orange to orange-yellow, pedicels 3–17(–25) mm; leaves 7–11.5 mm wide.

11. Pedicels 4–17(–25) mm, attached asymmetrically to calyx base (offset to one side); foliage not densely congested (internodes relatively elongate); southwestern Oregon to southwestern California ..... 3. **Diplacus aurantiacus**

11. Pedicels 3–5(–8) mm, attached symmetrically to calyx base; foliage densely congested (internodes relatively short); Cedros Island, Baja California ..... 4. **Diplacus stellatus**

10. Corollas pale yellow to orange-yellow or light orange; pedicels 4–6 mm; leaves 3.5–8 mm wide.

12. Orange, Riverside, and San Diego cos. ..... 12. **Diplacus x australis**

12. Santa Barbara Co. and extreme s San Luis Obispo Co. ..... 13. **Diplacus x lompocensis**

1. **Diplacus clevelandii** (Brandegee) Greene, Erythea 4: 22. 1896. *Mimulus clevelandii* Brandegee, Gard. & Forest 8: 134, plate 20. 1895. **TYPE: USA. California.** San Diego Co.: Cuyamaca Peak [protologue: "on the south side ... not far from the signal station on its summit. .. elevation over 6000 feet"], 7 Jul 1894, *T.S. Brandegee s.n.* (holotype: UC digital image!, photo PH; isotypes: DS digital image!, GH, POM, SD, US digital image!).

Distribution. Orange, Riverside, and San Diego cos.; Baja California.

2. **Diplacus aridus** Abrams, Bull. Torrey Bot. Club 32: 540. 1905. *Mimulus aridus* (Abrams) A.L. Grant, Ann. Missouri Bot. Gard. 11: 336. 1924. **TYPE: USA. California.** San Diego Co.: dry ridges, Jacumba, near the monument, 31 May 1903, *L. Abrams 3656* (holotype: NY digital image!; isotypes: BM, CAS digital image!, E, F digital image!, GH 2 sheets, K, MO digital image!, NY digital image!, PH digital image!, POM, RSA, UC-2 sheets, US digital image!).

Distribution. Imperial and San Diego cos.; Baja California.

3. **Diplacus aurantiacus** (Curtis) Jeps., Man. Fl. Pl. Calif. 919. 1925. *Mimulus aurantiacus* Curtis, Bot. Mag. 10: plate 354. 1796 (not *M. aurantiacus* Renjifo; see Grant 1924, p. 146). *Diplacus glutinosus* var. *aurantiacus* (Curtis) Lindl., Paxt. Fl. Gard. 3: plate 92. 1851. **NEOTYPE** (Thompson 2005, p. 149): **USA. California**. "Hort. Kew, 1795, ex California," without collector or number (BM!, photo UC!). In selecting the neotype, Thompson noted this: "In the protologue Curtis does not describe or mention fruits or seeds and states 'flowered this Summer with Mr. Covill, Nurseryman, King's-Rd. [...] We know not with certainty of what country it is a native.' The neotype I have selected for *Mimulus aurantiacus* is appropriate, because it is cultivated material preserved in 1795. Even if it is not Covill's material and Curtis never saw this specimen, it probably came from the same wild-collected seed source as his material, given the difficulties of acquiring material from California at the time."

Mimulus glutinosus J.C. Wendland, Bot. Beob., 51. 1798. *Diplacus glutinosus* (J.C. Wendland) Nutt., Ann. Nat. Hist. 1: 138. 1838. **TYPE: USA. California**. According to Thompson (2005. p. 151), "a collection taken from cultivated material in the Wendland Herbarium, without collector or date (**neotype**: GOET, scanned image!)."

Diplacus leptanthus Nutt., Ann. Nat. Hist. 1: 138. Apr 1838, 'leptantha? [also: Bot. Mag. 65: plate 3655. 1 May 1838]. *Mimulus leptanthus* (Nutt.) A.L. Grant in L.H. Bailey, Gentes Herb. 1: 136. 1923. **TYPE: USA. California**. "herb. Schw. sub nom. 'M. glutinosus Mendoza-Hook.,' *Diplacus leptantha* Nutt.," [protologue: at PH; "communicated to the late Mr. Schweinitz by Sir William Jackson Hooker, and marked *'Mimulus glutinosus* from Mr. Menzies'"] (holotype: PH digital image!, photo UC). Synonym of *Diplacus aurantiacus*, fide Thompson (2005, p. 152); = *Mimulus linearis* Benth., fide Bentham (1868, p. 368); = *Mimulus longiflorus* var. *linearis*, fide Grant (1924, p. 334).

Diplacus latifolius Nutt., Ann. Nat. Hist. 1: 138. April 1838 [also Bot. Mag. 65: plate 3655. May 1838]. *Diplacus glutinosus* var. *latifolius* (Nutt.) Greene, Pittonia 2: 155. 1890. **TYPE: USA.** California. [Monterey Co.:] [protologue]: "round Montersey [Monterey], Upper California, in April," [BM sheet]: "Santa Barbara," *T. Nuttall s.n.* (holotype: BM photo PH!; isotype: K).

Distribution. Oregon: Curry Co. California: Del Norte, Humboldt, Mendocino, Lake, Colusa, Sonoma, Napa, Yolo, Sacramento, Marin, Solano, Contra Costa, Alameda, San Francisco, San Mateo, Santa Cruz, Santa Clara, Monterey, Stanislaus, Merced, Eldorado, Amador, Calaveras, Tuolumne, San Luis Obispo, and Santa Barbara cos.

4. **Diplacus stellatus** Kellogg, Proc. Calif. Acad. Sci. 2: 18. 1863. *Diplacus glutinosus* var. *stellatus* (Kellogg) Greene, Pittonia 2: 155. 1890. *Mimulus stellatus* (Kellogg) A.L. Grant, Ann. Missouri Bot. Gard. 11: 337. 1924. **LECTOTYPE** (Thompson 2005, p. 152): **MEXICO. Baja California**. Cedros Island, *J.A Veatch s.n.* (GH; isolectotype: CAS). The holotype at CAS was destroyed.

Distribution. Baja California, known only from Cedros Island.

Diplacus stellatus is characterized by relatively small, orange-yellow corollas, nearly glabrous calyces, and short, nearly glabrous pedicels. McMinn distinguished it from *D. aurantiacus* in his key by corollas [limbs] less than 3/4 inch broad (vs. corollas 3/4 to 1 1/8 inches broad in *D. aurantiacus*). He noted that the epithet is a misnomer, as the stellate hairs on the abaxial leaf surfaces of the type specimen apparently are from other species, but the present study confirms the presence of stellate hairs in both *D. stellatus* and *D. aurantiacus*.

Thompson (2005) treated *Diplacus stellatus* simply as a synonym of *D. aurantiacus* var. *aurantiacus*, and morphological differences between them indeed are hardly pronounced. The far geographic disjunction of *D. stellatus*, however, and its proximity instead to other species suggests that similarities with *D. aurantiacus* may be convergent. The differences in internode and pedicels lengths and pedicel insertion (as in the key) provide a morphological basis for maintaining *D. aurantiacus* and *D. stellatus* as distinct.

5. **Diplacus grandiflorus** Groenland, Rev. Hort. [Paris] ser. 4, 6: 402, fig. 136. 1857 (not *Diplacus grandiflorus* Greene, 1890). *Diplacus longiflorus* var. *grandiflorus* (Groenland) Jepson, Man. Fl. Pl. Calif. 919. 1925. *Mimulus bifidus* Pennell, Proc Acad. Nat. Sci. Philadelphia 99: 168. 1947, nom. nov. (based on *D. grandiflorus* Groenland, blocked in *Mimulus* by *M. grandiflorus* Howell 1901 = *Erythranthe guttata*). **NEOTYPE** (Thompson 2005, p. 159): Hort. Muhlenpfordt, Hannover, G. Engelmann, 4 Jun 1857, collector not indicated (MO).

Thompson's choice of a neotype is justified and accompanied by the following comments (p. 161): "The protologue for *Diplacus grandiflorus* Groenland was published on 16 August 1857, according to printers notations (p. 389) for Vol. 6, No. 16 (pp. 389-416). The neotype I have selected for this name is dated 4 Jun 1857. ... The specimen seems to have come from Hannover, Germany, perhaps sent from Muehlenpfordt to Engelmann. Groenland mentions only unspecified cultivated material, and the neotype is cultivated material. Although there is no direct connection between this specimen and the protologue, it seems to be an appropriate neotype for Groenland's name. Even if Groenland never saw it, there is a good chance that it grew from the same seed source as his material, given the difficulties of acquiring seeds from California at that time."

Unfortunately, however, the origin of the cultivated plants represented by the specimen is likely to have been from Monterey Co. or San Luis Obispo Co., where various early collectors made visits — that is, the range of *Diplacus* x *linearis* (typified by a Douglas collection from a coastal locality in this area). If this can be shown to be the case, then *D. grandiflorus* Groenland would be recognized as a synonym of *D.* x *linearis* and the Sierran species would be without a name.

Diplacus glutinosus var. *grandiflorus* Lindl. & Paxton, Paxt. Fl. Gard. 3: 96, plate 92. 1852. *Mimulus aurantiacus* var. *grandiflorus* (Lindl. & Paxton) D.M. Thompson, Monogr. Syst. Bot. 75: 158. 2005. **NEOTYPE** (Thompson 2005, p. 158): **USA. California.** Butte Co.: Between Chico and Forest Ranch, elev. 2000 ft., 18 May 1914, *A.A. Heller 11407* (UC; isoneotypes: A, CAS, CU, DS, E, F, GH, MO, ND-G, NY, OSC, PENN, PH).

Diplacus grandiflorus Greene, Pittonia 2: 156. 1890, nom. illeg. (not *Diplacus grandiflorus* Groenland 1857). **LECTOTYPE** (Thompson 2005, p. 159): **USA. California.** [Nevada Co.:] On Yuba River, 5 Jul 1884, *E.L. Greene s.n.* (ND-G-1714; isolectotype: ND-G-1721). A photo of one or the other of the ND-G sheets is at PH!.

Distribution. Tehama, Butte, Plumas, Yuba, Sierra, Nevada, El Dorado, and Placer cos.

6. **Diplacus x linearis** (Benth.) Greene, Pittonia 2: 156. 1890. *Mimulus linearis* Benth., Scroph. Ind. 27. 1835 (as species). *Mimulus glutinosus* var. *linearis* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. *Mimulus glutinosus* forma *linearis* (Benth.) Voss in Vilmorin, Vilm. Blumengartn. (ed. 3) 1: 762. 1895. *Mimulus longiflorus* var. *linearis* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 334. 1924. *Diplacus longiflorus* var. *linearis* (Benth.) McMinn, Man. Calif, shrubs (ed. 1) 498. 1939. **TYPE**: **USA. California.** No other collection data, *Douglas s.n.* (holotype: K-herb. Bentham; isotypes: BM, E, GH, K-herb. Hooker, NY digital image!, OXF). Douglas's itinerary in 1832 included localities in Santa Cruz, Monterey, San Luis Obispo, and Santa Barbara counties.

Mimulus bifidus subsp. *fasciculatus* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 168. 1947. *Diplacus fasciculatus* (Pennell) McMinn, Madroño 11: 70, 73. 1951. **TYPE: USA. California**: Monterey Co.: Rocky hills, Santa Lucia Park, Arroyo Seco, alt. 2500 ft, 10 May 1936, *L.S. Rose 36278* (holotype: PH; isotype: US).

Distribution. Monterey, San Benito, and San Luis Obispo cos.

These plants were allied by Pennell (1947, p. 168) with the Sierran *Diplacus grandiflorus* Groenland (= *Mimulus bifidus* Pennell), as "a narrower-leaved and smaller-flowered subspecies," and they were considered synonymous by Thompson (2005), but the two are disjunct in geography (Figs. 3 and 4) and ecology. The molecular analysis by Beardsley et al. (2004) suggests that *D. grandiflorus* is related as a sister to *D. aurantiacus*.

Diplacus grandiflorus and *D.* x *linearis* appear to be distinct as a pair particularly in the notching of the upper corolla lobes, but morphology and geography suggest that the parents of *Diplacus* x *linearis* are *D. calycinus* and *D. aurantiacus*, thus *D. grandiflorus* and *D.* x *linearis* are not each other's closest relatives. McMinn (1951a) regarded *Diplacus* x *linearis* as a hybrid between *D. aurantiacus* and *D. fasciculatus*, the latter treated by him as a distinct species and separate from the Sierran *D. grandiflorus*.

7. **Diplacus calycinus** Eastw., Bot. Gaz. (Crawfordsville) 41: 287. 1906. *Mimulus longiflorus* var. *calycinus* (Eastw.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 331. 1924. *Diplacus longiflorus* var. *calycinus* (Eastw.) Jeps., Man. Fl. Pl. Calif. 919. 1925. *Mimulus longiflorus* (subsp. *calycinus* (Eastw.) Munz, Aliso 4: 99. 1958. **TYPE: USA. California**. Tulare Co.: South Fork Kaweah River, 6000 ft, 22 Jul 1904, *G.N. Culbertson 4407* [distributed by C.F. Baker, No. 4407] (holotype: CAS digital image!; isotypes: CAS digital image!, GH, K, MO digital image!, NY digital image!, PH digital image!, POM, UC, US digital image!).

Distribution. San Luis Obispo, Los Angeles, San Bernadino, and Riverside cos., separated from a Sierran population system in Fresno, Tulare, and Kern cos.

Although first described as a separate species, *Diplacus calycinus* has more recently been treated at subspecific or varietal rank within *D. longiflorus* (Grant 1924; Pennell 1951; Munz 1973). Thompson (2005) went even further in including *D. calycinus* simply as a synonym within his concept of *Mimulus aurantiacus* var. *pubescens* (= *D. longiflorus*), but results from the Tulig PCA and DFA indicate that *D. calycinus* is distinct from *D. longiflorus*, especially in corolla length, corolla tube length, and style length. Corolla color is cream to pale yellow in *D. calycinus* and salmon in *D. longiflorus*.

Diplacus calycinus and *D. longiflorus* are essentially allopatric to parapatric. Particularly in Fresno, Tulare, and Kern cos., where *D. calycinus* occurs completely separated from *D. longiflorus* (see Thompson's Fig. 63), it appears to be clearly distinct especially in abaxial leaf vestiture — the hairs are unbranched, broad, and vitreous, compared to the branched, thinner, and dull hairs of *D. longiflorus*. The type of *D. calycinus* is a Sierran plant from Tulare County.

Overlap between the two taxa occurs only in southern California, especially in the region (in San Bernadino Co.) connecting the San Gabriel and San Bernardino mountains. In that area, flower color of individuals of *D. calycinus* ranges from light to dark orange, and corolla length is shorter.

10. **Diplacus longiflorus** Nutt., Ann. Nat. Hist. 1: 139. 1838. *Mimulus longiflorus* (Nutt.) A.L. Grant, Gentes Herb. 1: 136. 1923. **TYPE: USA. California.** [Santa Barbara Co.:] [protologue]: "in rocky places by small streams, in the vicinity of Sta. Barbara," Apr [1836], *T. Nuttall* s.n. (holotype: BM photo PH!; isotypes: GH, K). Noted by Nuttall as "A species remarkable for the width and very oblique emargination of the lobes of the corolla, which is of a paler yellow than in any other species, and inclining to a fawn color. The stems are very leafy, pubescent, and the leaves elongated and acuminate. The base of the calyx is also almost lanuginous."

Diplacus glutinosus var. *pubescens* Torrey, Pacif. Railr. Rep. 7(3): 15. 1857. *Mimulus aurantiacus* var. *pubescens* (Torrey) D.M. Thompson, Syst. Bot. Monogr. 75: 161. 2005. **TYPE: USA. California.** Lieut. Parke's Expedition, between San Bernardino and San Diego, Apr 1854-55, *Dr. Antisell 176* (holotype: NY digital image!).

Mimulus glutinosus var. *brachypus* A. Gray in W.H. Brewer, S. Watson, & A. Gray, Bot. California 1 (ed. 1): 566. 1876. **LECTOTYPE** (Thompson 2005, p. 162): **USA. California.** "California," *J.N. Coulter 639* (GH; isolectotypes: E, K-2 sheets).

Diplacus arachnoideus Greene, Calif. Acad. Sci. 1: 210. 1885. **LECTOTYPE** (Thompson 2005, p. 000): **MEXICO. Baja California.** All Saints' Bay [Bahia de Todos Santos], 16 Apr 1885, *E.L. Greene s.n.* (UC digital image!; isolectotypes: BM, GH, ND-G photo PH!). The holotype at CAS was destroyed.

Diplacus speciosus Davy, Erythea 2: 101. 1894. **TYPE: USA. California.** Cultivated at Berkeley ["Botanic Garden of the University of California"], Jun 1894, *J. Burt Davy s.n.* (holotype: UC digital image!; isotypes: ND-G, US digital image!). According to the protologue, the plants originally came from Humboldt County, but the loosely villous calyx vestiture indicates, in contrast, that its origin was much further south.

Distribution. San Luis Obispo, Santa Barbara, Ventura, Los Angeles, Orange, San Bernadino, Riverside, San Diego cos.; Baja California. Plants cited and mapped as *Mimulus aurantiacus* var. *pubescens* by Thompson (2005) from Fresno, Tulare, and Kern cos. are identified here as *Diplacus calycinus* (see comments above).

11. **Diplacus rutilus** (A.L. Grant) McMinn, Madroño 11: 83. 1951. *Mimulus longiflorus* var. *rutilus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 333. 1924. *Diplacus longiflorus* var. *rutilus* (A.L. Grant) McMinn, Man. Calif. Shrubs, 498. 1939. **TYPE: USA. California.** Ventura Co.: Santa Susanna Pass, dry hillsides, 10 Jun 1920, *A.L. Grant 1650* (holotype: MO digital image!; isotypes: CAS, CU, GH, JEPS, K, NY-2 sheets digital images!, OSC, PH, POM, UC, US digital image!).

Distribution. Ventura, Los Angeles, and Riverside cos.

Diplacus rutilus was treated by McMinn (1951a) as a distinct species, one among three red-flowered species in the genus (corolla lobe margins tinged with yellow in *D. rutilus*). It was distinguished in his key by pedicels less than 3/8 inches long and glandular-hairy (vs. pedicels 3/8–1 inch long and glabrous in *D. puniceus* and *D. parviflorus*). He cited collections of *D. rutilus* from Ventura, Los Angeles, and Riverside counties. Beeks (1962, p. 120) noted that "the Santa Susanna Pass population in northeastern Ventura county ... with their deep velvety red flowers, are considered to constitute only a form of *D. longiflorus*." Munz 1973 treated these plants as a variety of *D. longiflorus*, noting that they occur "with the sp. particularly in interior Los Angeles Co., less so in Ventura and Riverside cos." Thompson (2005) described the corolla color of [D.] *longiflorus* as "pale yellow" but placed *D. rutilus* as a synonym of that species without comment.

Diplacus rutilus is similar to typical *D. longiflorus* with respect to quantitative characters but was located infrequently in the field by Tulig. Measurements of populations with these red variants were not treated with *M. longiflorus* as a whole in the statistical analyses. Here, however, we hypothesize that these plants, surely distinct also in biology from yellow-flowered *D. longiflorus* and with a coherent albeit limited geographical distribution, appear to be justifiably treated at specific rank. They obviously need urgently to be studied and evaluated from the perspective of conservation.

12. **Diplacus x australis** (McMinn ex Munz) Tulig, **comb. nov.** *Diplacus australis* McMinn, Madroño 11: 58, 60, plate 12. 1951 (as species), nom. illeg. (without Latin diagnosis). *Mimulus aurantiacus* subsp. *australis* McMinn ex Munz, Aliso 4: 98. 1958. *Diplacus aurantiacus* subsp. *australis* (McMinn ex Munz) Beeks ex Thorne, Aliso 9: 194. 1978. **TYPE: USA. California**: San Diego Co.: Descanso Grade, Jun 1906, *K. Brandegee s.n.* (holotype: UC digital image!). McMinn cited a type (as above) but gave no Latin diagnosis, as he explicitly intended the epithet "australis" to be a *nomen novum* for *Mimulus linearis* Benth. (and its combined forms, see below), which he noted had been misapplied to the plants he was now referring to as *D. australis*. Munz, in recognizing the lack of a Latin diagnosis, provided one of his own, but he (Munz), in turn, cited no type — crediting McMinn for the basionym and providing the full citation for McMinn's attempt to validate the name.

Distribution. Orange, Riverside, and San Diego cos.; Baja California.

The placement of *Diplacus* x *australis* among hybrid/intermediate populations in both the PCA and DFA indicate that it is likely of hybrid origin. It is similar to *D. longiflorus* in overall flower morphology, including color, and its geographic distribution in southern California between *D. longiflorus* and *D. puniceus* suggests that Thompson's hypothesis (2005) that those two are the parents is reasonable (*Mimulus aurantiacus* var. *pubescens* x *M. aurantiacus* var. *puniceus* in his taxonomy, or *M. longiflorus* x *M. puniceus*).

Beeks (1962) noted that there is a pubescent race (the "San Gabriel race") of *Diplacus longiflorus* and a glabrous race (the "San Diego race") — the latter is interpreted here as essentially *D.* x *australis*. Calyx, pedicel, cauline, and leaf vestiture of *D.* x *australis* varies from glabrous to sparsely puberulent or short-villous. Corollas tend to have a narrower tube and limb. On the other hand, corolla color is longiflorus-like in almost all of these variants, including most plants identified by Thompson as intermediate between *D. longiflorus* and *D. puniceus*. A very small percentage appear (from herbarium collections) to have intermediate color. Munz (1973) described the corolla color of "subsp. *australis*" as orange-yellow to light apricot or buff or white."

Diplacus x *australis* and *D.* x *lompocensis* can be generally separated from *D. longiflorus* by their smaller corolla features and by much-reduced calyx (and other) pubescence, but the two putative hybrids are similar to each other in most other features. There are no obvious qualitative morphological distinctions between the two putative hybrids and they are only easily separated by geographic range.

As discussed above, Streisfeld and Kohn (2005) found that in San Diego County, *Diplacus longiflorus* (as identified here) and *D. puniceus* are discrete in morphology and separate in geography, separated by a narrow zone of hybrids and putative introgressants, among which *D.* x *australis* is included.

In the Tulig studies, hybrid populations in San Diego Co. show intermediate features on PC1 between *puniceus* and *longiflorus*. They also show a range of flower color from the red of *puniceus* to the orange of *australis* with various shades in between. These results confirm the findings of Waayers (1996) and that a zone of introgression exists between the coastal and inland populations and are in agreement with those of Streisfeld and Kohn (2005).

Thompson's Figure 65 (p. 163), which maps 126 herbarium specimens of these plants in San Diego County, shows a much broader zone of intermediates with the few yellow-flowered non-intermediates restricted mostly to the eastern extremity of the range and identified as *Diplacus longiflorus* (*Mimulus aurantiacus* var. *pubescens* in Thompson's taxonomy). *Diplacus puniceus* is shown as distributed in a broad and relatively discrete band in the west (near-coastal), corresponding to the observations of Waayers, Tulig, and Streisfeld and Kohn.

The same pattern, however, does not appear to hold for *Diplacus puniceus* and *D. longiflorus* in Baja California, either as mapped by Thompson (Fig. 65) or as mapped in the present account (Fig. 7, based on collections from SD, ARIZ, and TEX). Instead, based on Thompson's criteria and using many SD specimens annotated by him, *D. puniceus*, *D. longiflorus*, and putative intermediates (*D.* x *australis*) appear to be broadly sympatric. Most of the putative intermediates have both corolla color and morphology similar to typical *D. longiflorus* — Thompson's assessments of intermediacy apparently were weighted toward reduction in leaf width and in vestiture.

Only two Baja California collections were encountered that have the vegetative and floral morphology of *Diplacus* x *australis* but with red or reddish corollas, clearly suggesting the genetic influence of *D. puniceus*: S of San Vicente, *Pennell & Epling 25240* (SD) and 2 mi NW of San Antonio [32° 00' N, 116° 40.5' W], *Moran 13954* (SD). Otherwise, collector's notes for specimens mapped here as D. x *australis* describe corolla color as salmon, salmon yellow, pale yellow, pale orange-yellow, light orange, and pale orange.

Among the most significant problems needing further study in sect. *Diplacus* is the degree of variability in vestiture in *D. longiflorus* as related to the definition of *D.* x *australis*. Are yellow-flowered plants with reduced vestiture more accurately regarded as populational variants of D. longiflorus?

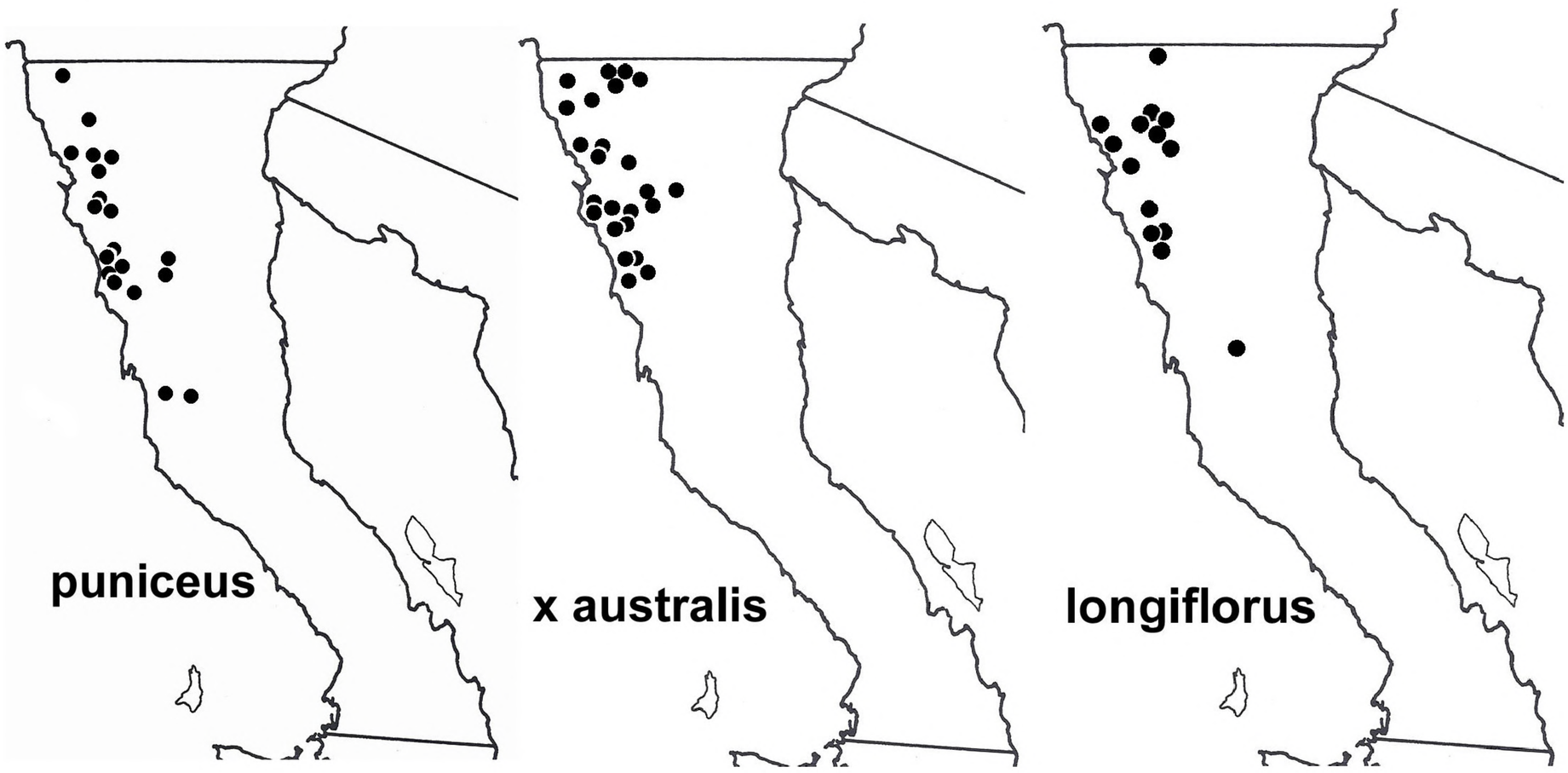

Figure 7. Distribution of *Diplacus puniceus*, *D.* x *australis*, and *D. longiflorus* in Baja California.

13. **Diplacus x lompocensis** McMinn, Madroño 11: 62. 1951 (as species). *Mimulus aurantiacus* subsp. *lompocensis* (McMinn) Munz, Aliso 4: 99. 1958. **TYPE: USA. California**: Santa Barbara Co.: edge of open woods along Highway between Lompoc and Las Cruces, Santa Inez Mountains, 7 Jun 1949, *H.E. McMinn 5601* (holotype: UC digital image!).

Distribution. Santa Barbara Co. and extreme southern San Luis Obispo Co. (see Thompson's Fig. 64, p. 160).

Diplacus x *lompocensis*, which occurs essentially between the geographic ranges of *D. aurantiacus* and *D. longiflorus* in southern Santa Barbara County, is perhaps the result of hybridization between these species (this also was Thompson's interpretation). It has intermediate floral features between these species on PC1. Stable populations of the putative hybrid are found throughout this region, although at either end of its distribution, populations may more closely resemble the nearer parent. Considering that both *D. aurantiacus* and *D. longiflorus* are morphologically consistent across broad regions, *D.* x *lompocensis* is perhaps best interpreted as a stable zone of introgression.

Although the origin of *Diplacus* x *lompocensis* is different, its difference from *D.* x *australis* is quantitative and much-overlapping, mostly in corolla features. The two are only easily separated by geographic range.

0. **Diplacus puniceus** Nutt., Ann. Nat. Hist. 1: 137. 1838. *Mimulus puniceus* (Nutt.) Steud., Nomencl. Bot. (ed. 2) 2: 150. 1841. *Diplacus glutinosus* var. *puniceus* (Nutt.) Benth. in DC., Prodr. 10: 368. 1846. *Mimulus glutinosus* var. *puniceus* (Nutt.) A. Gray, Bot. California 1: 566. 1876. *Mimulus aurantiacus* var. *puniceus* (Nutt.) D.M. Thompson, Syst. Bot. Monogr. 75: 156. 2005. **TYPE: USA. California**: San Diego Co.: St. Diego [San Diego, 1836], *T. Nuttall s.n.* (holotype: BM; isotypes: K, PH digital image!).

Distribution. Los Angeles, San Bernadino, Orange, Riverside, and San Diego cos.; Baja California. A red-flowered plant from Sierra Co., apparently from a natural habitat, annotated by D.M. Thompson as *Mimulus aurantiacus* var. *puniceus* needs to be studied further (28 May 1988, *Pitzer, Morgan, and Soldan 903*, UCR).

0. **Diplacus parviflorus** Greene, Pittonia 1: 36. 1887. *Mimulus parviflorus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 344. 1925 (not *Mimulus parviflorus* Lindley 1825). *Mimulus aurantiacus* var. *parviflorus* (Greene) D.M. Thompson, Syst. Bot. Monogr. 75: 157. 2005. *Mimulus flemingii* Munz, Man. S. Calif. Bot., 477, 601. 1935, nom. nov. (blocked by *Mimulus parviflorus* Lindley). **LECTOTYPE** (Thompson 2005, p. 157): **USA. California.** Santa Barbara Co.: [protologue: "north side of] Santa Cruz Island, Jul and Aug, 1886, *E.L. Greene s.n.* (UC digital image!; isolectotypes: A, BM, DS digital image!, F digital image!, possible type GH, MO, ND-G-2 sheets, NY-3 sheets digital images!, PENN, PH digital image!, UC-2 sheets digital images!, US).

Distribution. (Channel Islands) in Santa Barbara, Ventura, and Los Angeles cos.

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